PHYLOGENETIC RECONSTRUCTION OF THE NEOTROPICAL FAMILY QUIINACEAE (MALPIGHIALES) BASED ON MORPHOLOGY WITH REMARKS ON THE EVOLUTION OF AN ANDRODIOECIOUS SEX DISTRIBUTION[1]

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Abstract

Based on morphology, a cladistic analysis of the Neotropical family Quiinaceae (Malpighiales) was performed to generate a hypothesis of the phylogenetic relationships within the family. The monotypic Medusagynaceae and four species of Ochnaceae were used as outgroup. Using equal weights, the Quiinaceae find strong jackknife support and all genera, apart from *Lacunaria,* are monophyletic. *Lacunaria* receives support only after successive weighting. The aberrant species *Lacunaria oppositifolia* and *Quiina pteridophylla* are positioned within their respective genera, although separation of the former as monotypic cannot be discarded with certainty. Proposed close relationship of the two species is rejected. *Froesia* is the morphologically most distinguished genus and sister to all other taxa of the family. *Touroulia amazonica,* once suggested to be recognized at the generic level, forms a small but closely related clade with *T. guianensis. Quiina* is the most diverse and derived genus with highly unresolved relationships and numerous polymorphic characters. A reduction toward smaller inflorescences and flowers, fewer stamens, and fewer carpels can be hypothesized. Concerning the evolution of sex distribution, androdioecy was fixed early in a common ancestor of *Lacunaria, Quiina,* and *Touroulia,* and subsequently dioecy evolved in *Lacunaria.*

Key words: Androdioecy, *Froesia, Lacunaria,* morphology, phylogenetic analysis, *Quiina,* Quiinaceae, *Touroulia.*

The Quiinaceae are a Neotropical dicotyledonous family of 51 species, including several taxa not yet described. It presently comprises *Froesia* Pires (5 species), *Lacunaria* Ducke (10 species), *Quiina* Aubl. (34 species), and *Touroulia* Aubl. (2 species). The Quiinaceae occur principally in primary lowland rainforests, with a few species found in premontane and cloud forests, reaching an elevation of about 1500 m a.s.l. The family is distributed from Belize and Jamaica to southern Brazil and Bolivia with a center of diversity in the Amazon lowland forests (Fig. 1), and it comprises shrubs or medium-sized trees. While the systematic position of the family within the Malpighiales seems to be comparatively clear, recent studies have proposed embedding Quiinaceae in Ochnaceae on the basis of a single gene, the *rbc*L (Chase et al., 2000; Savolainen et al., 2000). However, this systematic amalgamation may not find support if additional molecular markers and/or morphology are considered (e.g., Soltis et al., 2000; Jansen et al., 2001). The infrafamilial systematics, despite the important contributions of Pires (1948, 1950, 1953, 1960), still raises many questions due to our incomplete knowledge of the family, an issue we wish to address in this paper.

Circumscription and mutual relationships of the genera of Quiinaceae are issues not hitherto inves-

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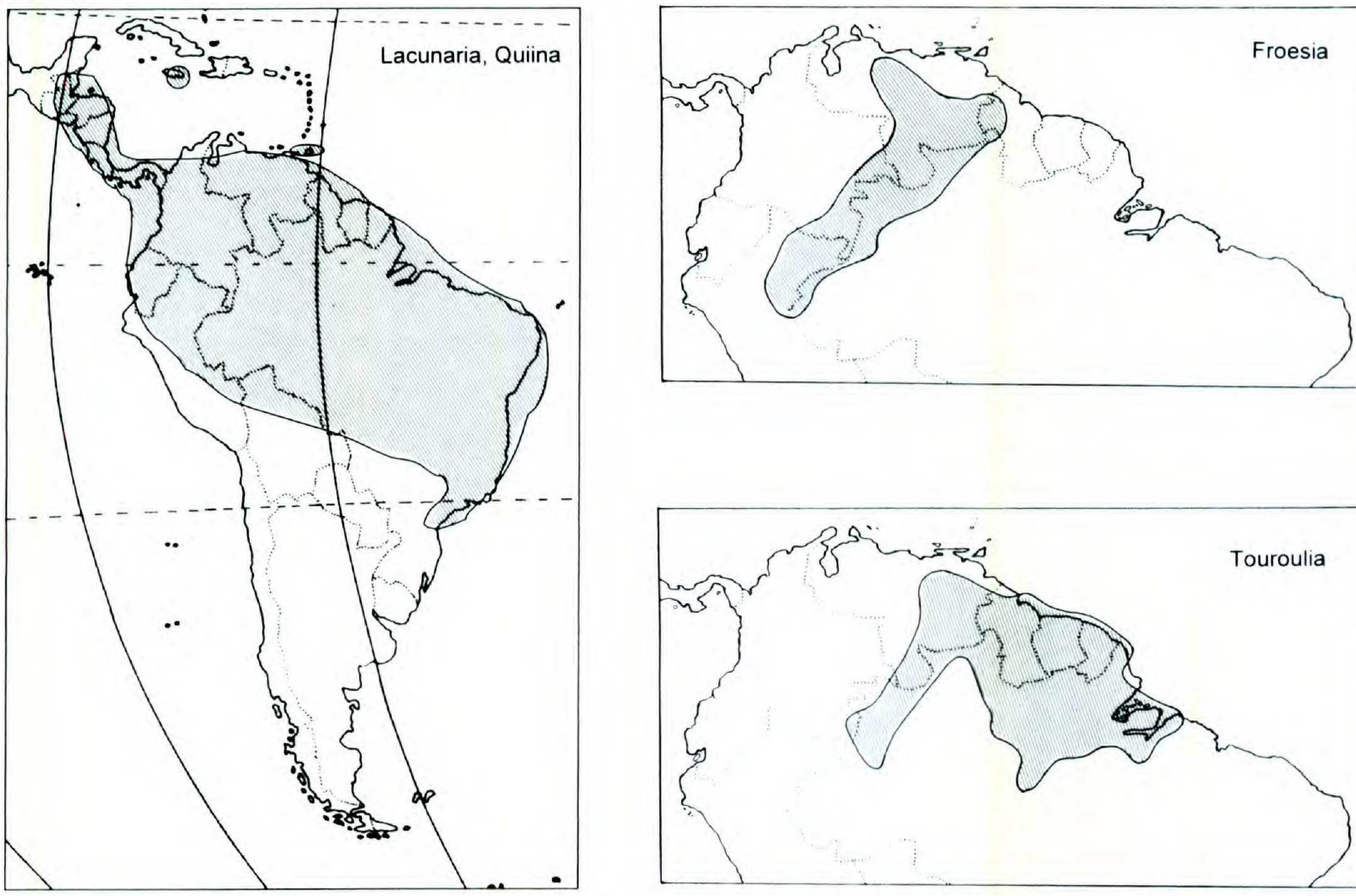

Figure 1. Distribution of the neotropical family Quiinaceae: *Lacunaria* and *Quiina*, circumscribing 10 and 35 species, respectively; *Froesia* with 5 species; and *Touroulia*.

tigated in a cladistic framework. Based on anatomical data, *Froesia* was postulated to have a somewhat isolated position in the family (Gottwald & Parameswaran, 1967). While *Froesia* forms a homogeneous, easily identified group, the two *Touroulia* species differ from each other, especially in anatomical characters, and the question arises whether they form a monophyletic group. Delimitation of species and generic boundaries are especially difficult to discern in *Quiina* and *Lacunaria*. The latter is comprised of a "core group" of similar species plus a few species more or less aberrant. The systematic position of *Lacunaria oppositifolia* Pires is uncertain, and generic rank for this taxon has been proposed (Pires, in sched.). Similarly, generic rank was proposed for *Touroulia amazonica* Pires & A. S. Foster (Pires, in sched.). *Quiina pteridophylla* (Radlk.) Pires is another puzzling species, being intermediate between *Quiina* and *Lacunaria* in several morphological characters.

In flowering plants, sex distribution is an important character for understanding the evolution of androdioecy and dioecy. Evolutionary hypotheses concerning mating systems have been postulated and reviewed in the light of population genetics (sexual selection, sex allocation theory) (Ross, 1978, 1982; Bawa, 1980; Thomson & Barrett, 1981; Charlesworth, 1984; Thomson & Brunet, 1990; Richards, 1997; Pannell, 1997) or phylogenetic constraints (Swensen et al., 1998). As evidenced by the existence of androdioecy (and dioecy) in different, rather divergent major taxa, it most probably originated independently and several times from hermaphroditism (Swensen et al., 1998). Careful examination shows that most of these species are only morphologically androdioecious, but functionally dioecious because of inviable pollen or indehiscent anthers. Functional androdioecy is very rare in seed plants. According to Swensen et al. (1998) it is known only from four species: *Datisca glomerata* (C. Presl) Baill. (Datiscaceae), *Mercurialis annua* L. (Euphorbiaceae), *Saxifraga cernua* A. Gray (Saxifragaceae), and *Phillyrea angustifolia* L. (Oleaceae). An additional species, *Schizopepon bryoniifolius* Maxim. (Cucurbitaceae), was reported by Akimoto et al. (1999). In Quiinaceae, *Froesia* has perfect flowers, *Touroulia* and *Quiina* are androdioecious, and *Lacunaria* is dioecious. The morphologically androdioecious genus *Quiina* is probably functionally dioecious too, producing inaperturate pollen in morphologically hermaphroditic plants (Pires, cited after Kubitzki, 1995 pers. comm.; Schneider, 1998).

With respect to the monophyly of Quiinaceae, all species share a characteristic combination of anatomical characters of wood and bark (Gottwald &

Table 1. Characters and character states for the Quiinaceae and the outgroups *Elvasia*, *Ouratea* (Ochnaceae), and *Medusagyne* (Medusagynaceae).

1. Plants not caulirosulate (0); caulirosulate (1).
2. Terminal internodes terete (0); laterally conspicuously compressed (1).
3. Leaves alternate (0); opposite (1); verticillate (2).
4. Adult leaves simple (0); compound (1).
5. Leaf rachis absent (0); not alate (1); alate (2).
6. Leaf blade or leaflet ovate (0); elliptic (1); obovate (2).
7. Leaf blade or leaflet glabrous or principal vein pubescent (0); principal vein and leaf surface along the veins pubescent (1); abaxial surface pubescent (2).
8. Leaf or leaflet apex acuminate to acute (0); obtuse (1); retuse (2).
9. Leaf or leaflet margin revolute (0); flat (1).
10. Leaf or leaflet margin entire (0); minutely serrulate (1); serrate (2).
11. Leaf or leaflet vein apices not protruding or reaching the margin (0); conspicuously protruding from lamina margin into teeth (1).
12. Number of teeth less than secondary veins (0); more teeth than secondary veins (1); teeth equal in number to secondary veins (2); teeth absent (3).
13. Venation craspedodromous (0); camptodromous (1).
14. Prominence of leaf venation: abaxially more prominent (0); abaxially and adaxially ± equally prominent (1); adaxially more prominent (2).
15. Intersecondary veins not developed (0); conspicuously developed (1); present but not conspicuously developed (2).
16. Tertiary veins scalariform (0); parallel (1); plumose-reticulate (2); reticulate (3).
17. Stomata paracytic (0); anomocytic (1).
18. Stomata positioned on a flat abaxial surface (0); in small depressions (1).
19. Petioles canaliculate (0); terete (1).
20. Petiole base not conspicuously broadened (0); pulvinoid broadened, not distinguishable from upper part (1); pulvinoid broadened, distinguishable from upper part (2).
21. Stipules not interpetiolar (due to alternate phyllotaxis) (0); interpetiolar (1); absent (2).
22. Stipules free (0); partly fused with deep, subulate lobes (1); completely fused (2).
23. Stipules persistent (0); caducous (1).
24. Stipules glabrous (0); pubescent (1).
25. Stipules sessile (0); stipitate (1).
26. Stipule margins entire (0); serrulate (1).
27. Stipule lobe(s) cuspidate (0); acuminate to acute (1); obtuse (2).
28. Plants hermaphroditic (0); andromonoecious (1); androdioecious (2); dioecious (3).
29. Inflorescence terminal (0); axillary (1).
30. Inflorescence glabrous (0); inconspicuously pubescent with trichomes mostly <0.2 mm long (1); conspicuously pubescent (velvety, tomentose) with trichomes mostly >0.3 mm long (2).
31. Inflorescence branched with one main axis (0); branched with several axes, fasciculate (1); unbranched (2).
32. Staminate flowers absent (0); in groups of 1 to 3 on terminal branches (1); in groups of 4 to 12 on terminal branches (2).
33. Pedicel in upper part slightly widened to cylindrical (0); obconical (1).
34. Pedicel articulation between base and 1/3 of the length (0); clearly more than 1/3 of length (1).
35. Pedicel (upper part) glabrous (0); pubescent (1).
36. Sepals 2 or 3 (0); 4 (1); 5 to 8 (2).
37. Sepal texture membranous (0); coriaceous (1).
38. Sepals glabrous (0); margin pubescent (1); margin and abaxial surface pubescent (2).
39. Sepals monomorphic, size equal (0); heteromorphic, outer smaller than inner (1).
40. Petal aestivation imbricate (0); contorted (1).
41. Petal margin (best observed in bud) glabrous (0); pubescent (1).
42. Petals obovate (0); elliptical (1).
43. Petal apices rounded (0); notched (1).
44. Functional stamens in hermaphroditic or staminate flowers 10 to 25 (0); 30 to 80 (1); >100 (2).
45. Filaments basally free from petals (0); adnate (1).
46. Anthers (in outline) elongate, linear-oblong (0); narrowly elliptic (1); ± round (2).
47. Anthers opening by apical pores (0); longitudinal slits (1).
48. Gynoecium syncarpous (0); apocarpous (1).
49. Carpels 2 (0); 3 (1); 4 to 8 (2); 10 to 14 (3); >16 (4).

Table 1. Continued.

50. Ovules per locule 1 (0); 2 (to 4) (1).
51. Some ovules abort (0); all ovules develop to seeds (1).
52. Fruit a capsule (0); berry (1); follicle (2); schizocarp of mericarps (3); dry, indehiscent (4).
53. Fruit apex rounded, centrally ± concave (0); conical, ± acute (1).
54. Fruits not spotted (0); with yellowish spots (1).
55. Fruit pericarp in transverse section without lacunae (0); inconspicuous lacunae (1); conspicuous lacunae (2).
56. Fruits glabrous (0); pubescent (1).
57. Exocarp of mature fruits smooth (0); longitudinally furrowed by underlying lacunae (1); fruit appearing conspicuously ribbed (2).
58. Seeds glabrous (0); pubescent (1).
59. Seeds longer than wide, ellipsoid (0); as long as wide, globose (1).
60. Crystalliferous cells abundant, in long rows along the veins (0); not abundant, sometimes in groups near the veins (1).
61. Crystalliferous cells without special thickening of cell wall (0); always present, with u-shaped thickening (1).

Parameswaran, 1967). An unusual craspedodromous leaf venation with very closely spaced tertiary veins is found in *Touroulia*, *Froesia*, and *Lacunaria* (a slightly different pattern is observed in *Quiina*), a set of characters also regarded as unique to the family (Foster, 1950a, b, 1951; Roth, 1996; Zizka & Schneider, 1999). *Froesia* and *Touroulia guianensis* Aubl. display a characteristic u-shaped thickening of the cell wall (cristarque cells) (unpublished data). Another common character is the presence of mucilaginous cavities, particularly in petioles (Schofield, 1968), and is frequently observed in all genera.

Quiinaceae have formerly been regarded as part of the order Theales (Cronquist, 1981). More recently, phylogenetic studies based on DNA sequence data (*rbc*L, *atp*B, and 18S) place the family in Malpighiales (Fay et al., 1997; Källersjö et al., 1998; Litt & Chase, 1998; Nandi et al., 1998; Chase, 1996, pers. comm.). This position was accepted in the ordinal classification of the flowering plants recently published by the Angiosperm Phylogeny Group (APG, 1998). These studies suggest that the closest relatives of Quiinaceae are Ochnaceae and/or Medusagynaceae. Despite this affinity, the relationship between each of these families is weak. In the study by Nandi et al. (1998), Quiinaceae are sister to Ochnaceae when based solely on weighted *rbc*L parsimony. When combined with non-molecular data, Quiinaceae shift and lie basal to the sister pair of Ochnaceae and Medusagynaceae. The positioning of Medusagynaceae, Ochnaceae, and Quiinaceae within the Malpighiales was unstable depending on character sets used.

For the forthcoming treatment of Quiinaceae for the *Flora Neotropica* (Schneider & Zizka, in prep.), the present study based on morphology attempts to resolve questions of generic circumscription, including morphological synapomorphies. We also investigate the affinities of the aberrant species *Lacunaria oppositifolia*, *Quiina pteridophylla*, and *Touroulia amazonica*. Finally, we provide a familial interpretation of gynoecium morphology and sex distribution in a phylogenetic perspective.

Data and Methods

Taxa

Ingroup monophyly is necessary for correct rooting of the tree (Nixon & Carpenter, 1993). The outgroup was therefore chosen from the two most closely related families, Ochnaceae and Medusagynaceae (*Medusagyne oppositifolia* Baker). Gottwald and Parameswaran (1967) already pointed out that the most closely related family to Quiinaceae is Ochnaceae, and herein the tribes Elvasieae Engl. and Ourateeae Baill. of the former Exalbuminosae sensu Engler. Hence, two species each of the genera *Elvasia* DC. and *Ouratea* Aubl. were selected. Because information on infrageneric relationships within the outgroup is lacking, the species included in the analysis were selected according to the criteria of (1) their distribution within the geographical range of Quiinaceae, (2) their previous use in cladistic analyses (Amaral, 1991), and (3) the number of specimens available for detailed morphological and anatomical studies.

Within the ingroup, a total of 22 species were included as terminal taxa. Since the principal intention of the study was the resolution of generic relationships within the family, it was considered redundant to include all species. The present selection comprises representatives of all genera and, more importantly, all somewhat aberrant species as well as core representatives from *Lacunaria* and *Quiina*. *Froesia* is, on one hand, a comparatively

homogeneous group; on the other hand, it is the most distinct genus within the family. Thus, three species were chosen and regarded as sufficient because the inclusion of all its species would not change the principal topology of the cladogram. *Quiina* is represented by 12 out of its 34 species, many of which are difficult to diagnose and circumscribe because of remaining taxonomic and nomenclatural problems.

CHARACTERS AND CHARACTER STATES

Characters were extracted from morphological studies undertaken (see Table 1); the final data matrix appears in Table 2. Multistate characters are generally unordered in phylogenetic reconstruction, but if there is reason to believe a character state is intermediate between two other states, such a character may be ordered (Wilkinson, 1992, 1995). In our analysis, only two characters (6 and 8) could be treated as ordered. These refer to leaf outline and leaf apices where an intermediate transition state can be perceived. Unknown character states are coded with a question mark (?) and inapplicable states with a dash (-). Character evolution was traced by using the software MacClade (Maddison & Maddison, 1992).

Autapomorphies can either be included or excluded in phylogenetic reconstruction. Yeates (1992) argued that removal may also remove information from a data matrix, but Bryant (1995) disagreed, saying that they should be removed. Arguments against autapomorphies rest on the fact that they are unique, uninformative, and inflate the consistency index (CI). Phylogenetic reconstruction, however, is much more than consistency indices. This study, for example, aims to reconstruct the major evolutionary lineages within Quiinaceae with approximately a third of the species of *Quiina* sampled. To facilitate future studies using a wider sampling, autapomorphies were therefore included to avoid excluding potential synapomorphies.

Polymorphic characters are abundant in Quiinaceae and can be treated in different ways. For example, they could be coded as missing entries, which then introduce erroneous consistency indices and tree length (Nixon & Davis, 1991). Polymorphic characters could also be included and scored for the observed intraspecific variation, albeit a low phylogenetic signal (Wiens, 1995). Kornet and Turner (1999) recommended that polymorphic characters should be coded as plesiomorphic in favor of the observed intraspecific variation unless the ancestral state is unknown. Assessment of the ancestral state, at least in Quiinaceae, is a critical point and generally lacking. Since we believe that polymorphic characters do provide a phylogenetic signal and resolution, they are scored with the observed states.

Habit. Plants are caulirosulate in *Froesia*, which means that leaves are crowded at the stem or branch apex (char. 1).

Leaves. The presence of compound versus simple leaves (char. 4) is problematic with respect to homology and comparability of character states. For the current analysis the single leaflets of species with compound leaves are regarded as homologous to simple leaves because they are functionally equivalent units (Raunkiaer, 1934). Furthermore, this reflects the equivalent venation pattern of leaflets and simple leaves. Additional support is given by the presence of simple leaves in seedlings of pinnate-leaved *Froesia venezuelensis* Steyerm. & G. S. Bunting and pinnatifid leaves in seedlings of simple-leaved *Quiina pteridophylla*. In *Quiina* and *Lacunaria* the leaf margin (char. 10) can be inconspicuously serrulate, only seen with a strong lens (magnification $> 20\times$). In this case minute incisions or papillae are seen. The pattern of leaf venation is a peculiar and particularly important character in Quiinaceae (Foster, 1950a, b, 1951; Roth, 1996). All Quiinaceae exhibit a craspedodromous type (char. 13; classification following Hickey, 1973, 1979). The presence of conspicuous intersecondary veins (char. 15) discriminates *Quiina* and is regarded as a synapomorphy for the genus. Intersecondary veins have a diameter intermediate between secondary and tertiary veins; they originate from the primary vein and do not reach the leaf margins. In camptodromous *Medusagyne* it is hard to judge the intermediate veins as distinct intersecondaries. For the analysis they are considered as inconspicuously developed intersecondary veins. The tertiary venation pattern (char. 16) is unique to the Quiinaceae. In *Froesia, Lacunaria,* and *Touroulia*, the tertiary veins are densely spaced, strongly parallel, percurrent or, more frequently, anastomosing at different distances from their origin (e.g., Zizka & Schneider, 1999). In *Quiina* they are less parallel and more conspicuously branched, anastomosing with intersecondary or tertiary veins. This pattern is called plumose-reticulate according to Foster (1950a, b). A scalariform (ladder-like) pattern is observed in *Elvasia*.

Stipules. Stipules are always interpetiolar in Quiinaceae (char. 21), but the number of stipules or stipular lobes may differ among the genera (char. 22). Stipule number obviously varies with the phyllotaxis. In verticillate *Lacunaria* there is one stipule between neighboring petioles (as in verticillate *Q.*

Table 2. Data matrix of 61 morphological characters of the ingroup Quiinaceae and the outgroup, *Elvasia*, *Ouratea* (Ochnaceae), and *Medusagyne* (Medusagynaceae). In the matrix, inapplicable states are coded with a dash (-) and polymorphic taxa with letters: a = 0/1; b = 1/2; c = 0/2; d = 0/1/2; e = 2/3; ? = missing data.

Taxon	Character number						
	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6 1
OCHNACEAE							
Elvasia calophyllea A. DC.	0000010001	000000000a	0-000000a0	00000d0000	0a00000020	04000000?0	1
Elvasia elvasioides (Planch.) Gilg	0000010000	0300000000	0-000000a0	00000d0000	0a00000000	04000000?0	0
Ouratea lucens (Kunth) Engl.	0000010002	110112000a	0-000010a0	000002a001	0000000020	1300000000	1
Ouratea parviflora (DC.) Baill.	00000a000d	0001120000	0-000010a0	000002a001	0000000020	1300000000	0
MEDUSAGYNACEAE							
Medusagyne oppositifolia Baker	0010010212	0011231000	2------100	0?00021000	0001011041	0000002000	0
QUIINACEAE							
Froesia diffusa Gereau & Rod. Vásquez	10111aa0aa	0200010000	1101001002	0000121211	0012011111	02a01010a0	1
Froesia tricarpa Pires	10111a00a2	a200010010	110100100b	0000121211	0012011111	02001010a0	1
Froesia venezuelensis Steyerm. & G. S. Bunting	1011110002	0200010000	110100100b	0000121211	0012011111	02001010a0	1
Lacunaria crenata (Tul.) A. C. Sm.	00200b0002	a2000100ab	12110013ab	01a0111210	0001021021	0101201101	0
Lacunaria decastyla (Radlk.) Ducke	002001a002	12000100a1	121a001311	020a111210	000102103?	0100201101	0
Lacunaria jenmanii (Oliv.) Ducke	00200ba00a	03000100ad	121a0013a1	c20a111210	a10a021031	01?0201100	0
Lacunaria macrostachya (Tul.) A. C. Sm.	00200b000a	03000100a1	1211001312	0200111210	1001021031	0100201100	0
Lacunaria oppositifolia (Pires) Pires	0a100100a0	0300010011	101a0013a2	01a01b1211	1a00011021	0101200101	0
Quiina amazonica A. C. Sm.	0110010011	010012000c	1011001211	2100011110	1000121001	01a0101100	0
Quiina cruegeriana Griseb.	011001201a	0100120011	1011001212	1100021110	1a0a121001	0100101110	0
Quiina florida Tul.	0110010000	0300120001	10a1a01211	220aa11b10	10001210a1	0101100101	0
Quiina guianensis Aubl.	01100b0011	0101120011	101a00121a	111a011110	100a121001	01001011a0	0
Quiina longifolia Spruce ex Planch. & Triana	0110010000	0301120011	1001101211	2100021110	1001121001	0110101100	0
Quiina macrophylla Tul.	0110010000	0300120001	1011001212	21000a11a0	100a121001	01001011a0	0
Quiina obovata Tul.	0a10020c0a	0102120012	1001001211	11100b1110	100a121001	01001011a0	0
Quiina oiapocensis Pires	0110020a0a	0100120012	100110b212	2200121210	1a01?21001	0110111101	0
Quiina paraensis Pires & Fróes	0110010010	0300120001	101100221b	1100111210	10011210b1	0101100100	0
Quiina pteridophylla (Radlk.) Pires	002002cc1b	0101120012	120111a211	b100120110	1000121001	0100101100	0
Quiina rhytidopus Tul.	01100a0000	0300120101	1011001211	2100011b10	100a121001	0110101100	0
Quiina tinifolia Planch. & Triana	0110010000	0300120011	1011001211	2b000a11a0	100a121001	0100101100	0
Touroulia amazonica Pires & A. S. Foster	00112000ab	a200010010	1011001?01	0?00121211	0001021021	0100201100	0
Touroulia guianensis Aubl.	00112a00a2	1200010010	1c1a001201	0b01121ba1	00010210e1	0100201100	1

pteridophylla). In opposite-leaved *Quiina* and *Lacunaria oppositifolia* there are four per node (paired between petioles), while in opposite-leaved *Touroulia* only two per node are observed. In the latter, this apparently single stipule is interpreted as a product of paired fusion similar to cases observed in Rubiaceae (Goebel, 1932). In opposite-leaved *Froesia*, the two stipules per node are deeply divided into setose lobes. In Quiinaceae, stipules are present on the terminal node at least. If stipules are generally lacking on the more basal nodes they are coded as caducous (char. 23); if generally present on the three uppermost nodes they are treated as persistent.

Flowers. Sex distribution (char. 28) is heterogeneous in Quiinaceae, with *Froesia* being bisexual, *Lacunaria* unisexual and dioecious, and *Quiina* and *Touroulia* morphologically androdioecious, with male and hermaphroditic flowers on different plants. The number of sepals (char. 36) is variable in Quiinaceae. Four sepals are common and usually constant for a species, while species with five or more sepals display a higher variability in number. Less than four sepals is an exceptional condition and therefore given its own state.

The hermaphroditic *Froesia* flower bears numerous stamens, frequently more than 100 (char. 44). In the androdioecious genera, the staminate flowers generally produce 30 to 80 stamens, whereas the hermaphroditic flowers normally produce fewer. For coding, only the flowers with functional stamens are included in the analysis. Character 45, filaments free or adnate to the petals, only refers to the hermaphroditic flowers of species of *Quiina* because in that genus staminate flowers do not show this trait. Concerning the gynoecium (char. 48), *Froesia* is clearly apocarpous while *Ouratea* is syncarpous, because apocarpy is only gained during fruit development (Amaral, 1991). In *Lacunaria* and *Touroulia* the number of carpels (char. 49) is variable and relatively high (4 to 14), while in *Quiina* there are commonly 2 carpels. In the latter, only a few species (e.g., *Quiina florida* Tul., *Q. paraensis* Pires & Fróes) show transitional states with up to 5 carpels.

Fruits. The exocarp is usually longitudinally striate to furrowed by underlying resiniferous lacunae that are more or less conspicuous in transection (char. 57). In *Quiina florida* and *Q. paraensis*, the exocarp appears quite smooth and is not striated by the lacunae. Additionally, their fruits are spotted by a substance that looks like dried resinous exudate (char. 54).

Crystalliferous cells. One characteristic feature is the presence of the cristarque cells (char. 61), a term introduced by van Tieghem (1902). These are crystal-bearing cells with a conspicuous u-shaped wall thickening. They are often cited in familial descriptions (Cronquist, 1981, as solitary crystals; Amaral, 1991; Bhattacharyya & Johri, 1998; Kubitzki, 1995 pers. comm.) and hence could be erroneously assumed to be characteristic for the entire family. So far we were able to confirm them only for the genera *Froesia* (*F. tricarpa* Pires, *F. venezuelensis*) and *Touroulia* (*T. guianesis*), in accordance with the findings of Foster (1950b). In addition to these specialized cells, crystal druses can be regularly observed in the leaf tissue (char. 60).

PHYLOGENETIC ANALYSIS

The data matrix in Table 2, containing 27 taxa and 61 characters, was analyzed with PAUP* 4.0 for Macintosh (Swofford, 1998), using the branch and bound algorithm under the assumption of Fitch parsimony (Fitch, 1971). Multiple character states were interpreted as uncertain. An initial search was undertaken with equal weights saving all optimal trees. To evaluate characters with the strongest phylogenetic signal and to choose among equally parsimonious trees (Carpenter, 1988, 1994), successive weighting analysis (Farris, 1969) was undertaken after the initial search. The settings used the rescaled consistency or RC index (Farris, 1989), and to avoid fractions the base weight was set to 1000. The process was reiterated until the same tree length was obtained twice. A similar analysis was carried out where characters 6 and 8 were ordered.

Branch stability was estimated with Bremer support and jackknife analysis for both the equally weighted and weighted characters. Bremer support is defined as the number of extra steps necessary to lose a clade in the consensus tree, using the converse constraints approach (Bremer, 1988, 1994; Källersjö et al., 1992; Farris, 1996). Reweighted and rescaled branch support values calculate the robustness for each branch in the weighted consensus tree (Bremer, 1994; Gustafsson & Bremer, 1995). To ease the construction of all necessary constraints, the computer program AutoDecay 4.0 was used (Eriksson, 1998). Each constraint was estimated with a heuristic search of 100 replicates of random additions of the taxa (10 repetitions of each replicate), tree bisection-reconnection (TBR) branch swapping, holding five trees at each step, and saving all equally parsimonious trees. Jackknife (Farris & al., 1996) investigates the structure, or phylogenetic signal, in a matrix with-

out permutation, contrary to bootstrap (Felsenstein, 1985), but excludes an assigned fraction of characters, here set to 35%. The search strategy was set as for the Bremer support, but with 1000 replicates and saving no more than 100 trees.

Results

The analyses using morphology to infer the phylogeny of Quiinaceae yielded 1643 most-parsimonious trees using all characters as unordered as well as when characters 6 and 8 were ordered. The trees are 163 steps long (when ordered 164 steps) with an RI of 0.775 and a CI of 0.561, or 0.529 when uninformative characters were excluded (Fig. 2). Counting steps within the polymorphic taxa, the trees are 282 steps long, indicating numerous polymorphic characters.

Successive weighting of the characters yielded a stable result of 2 trees after three iterations, 73,206 steps long using unordered characters. This tree is a subset of the initial 1643, resulting in a consensus with a much better resolution of the otherwise collapsed genera *Lacunaria* and *Quiina*. Consensus of the primary 1643 trees and the 2 trees obtained after successive weighting together with jackknife fractions, Bremer support values, and weighted and rescaled support values, are shown in Figure 2. One of the most-parsimonious trees with characters optimized on the branches is shown in Figure 3.

Referring to the unweighted analysis, Quiinaceae form a well-supported monophyletic group, a grade from *Froesia* at the base to the most derived genus *Quiina*. Within the family, all genera are monophyletic except for *Lacunaria*, a genus completely collapsed to a comb. Based on equally weighted characters, no resolution within *Quiina* can be retrieved. The small genus *Touroulia* forms the sister to the *Lacunaria–Quiina* complex. Support for *Froesia* and *Quiina* must be regarded as strong, while support for *Touroulia* is moderate. No clear signal for a monophyletic *Lacunaria* can be retrieved, and *L. oppositifolia* attaches as sister to *Quiina*, a position with low jackknife support of 54%, but not found in the consensus (Fig. 2).

As to the weighted analysis, resolution is improved and only one trichotomy remains, the one in *Froesia*. All clades found in the equally weighted analysis are retrieved and, as a general trend, moderately or strongly supported groups are often better supported after successive weighting. *Froesia*, supported by a maximum jackknife value in the equally weighted analysis, needs five extra steps to be lost when unweighted, a value twice as strong after successive weighting. A similar situation is observed for *Touroulia*, and the support for *Quiina* increases almost three times. Using the weighting approach, *Lacunaria* is now found to be monophyletic, although with a Bremer support of only 0.9.

Discussion

Because a cladistic analysis can only elucidate ingroup relationships, we cannot put forward a hypothesis of relationships within the order Malpighiales, or determine whether Quiinaceae are sister to a paired Medusagynaceae–Ochnaceae, or sister to either one separately. Support for Quiinaceae is strong, with little difference in support values between equally weighted and weighted characters. This implies that several characters are initially strong and basal on the tree; these non-homoplasious synapomorphies include pubescent stipules (char. 24: 1), pubescent sepals (char. 38: 2), heteromorphic sepals (char. 39: 1), and a fruit exocarp with lacunae (char. 55: 1; Fig. 3). Other synapomorphies for Quiinaceae, addressed in the introduction, are the unique leaf venation pattern with densely spaced parallel or plumose-reticulate tertiary veins (char. 16) and the interpetiolar stipules (char. 21: 1).

In a molecular study of the relationships of *Medusagyne oppositifolia* by Fay et al. (1997), Quiinaceae were represented by *Quiina pteridophylla*, *Touroulia guianensis*, and *Lacunaria jenmanii* (Oliv.) Ducke, all included in our study. Contrary to our results, *Quiina* was found to be the most basal taxon in the family. *Quiina pteridophylla* is a morphologically aberrant species within the genus with some characters resembling species of *Lacunaria*, such as the phyllotaxis and the stipule number. Therefore it may be an inappropriate representative of *Quiina* and could attach as sister to all other genera due to long-branch attraction.

Froesia is indicated by our cladistic analysis to be the most basal genus in Quiinaceae, followed by a grade of *Touroulia*, *Lacunaria*, and *Quiina*. Particularly noteworthy is the apocarpous gynoecium (char. 48) of *Froesia*, a character state known neither from other Quiinaceae nor from Ochnaceae or Medusagynaceae. However, some Ochnaceae exhibit a secondary—otherwise called "ecological" (Baum, 1951)—apocarpy during fruit development (Amaral, 1991). In her cladistic analysis, Amaral (1991) interpreted this secondary apocarpy as a derived state differing from the states observed in the Quiinaceae and Scytopetalaceae (both families therein used as outgroups). Whether apocarpy in *Froesia* evolved secondarily is difficult to infer. The existence of a compitum, providing support for the

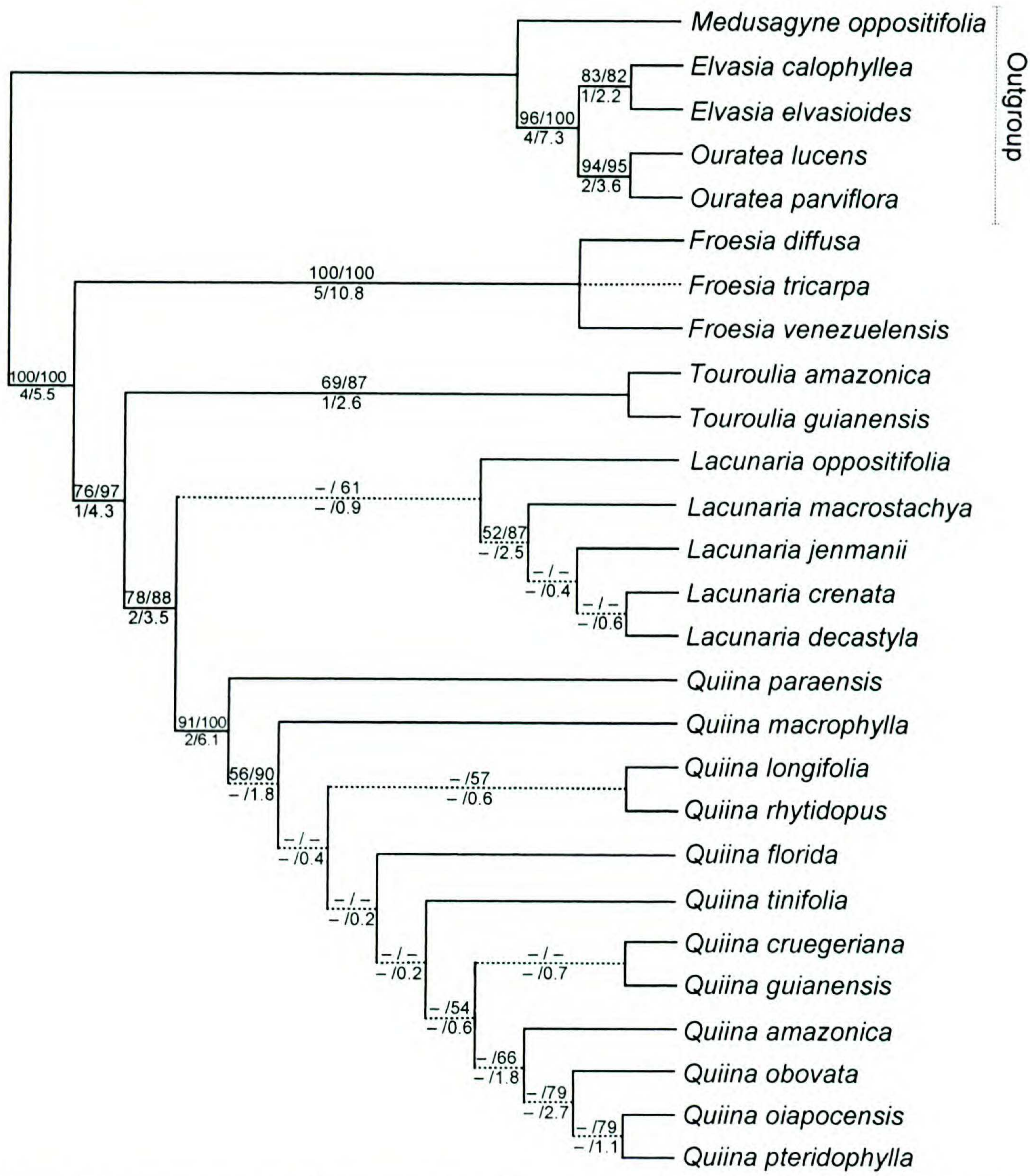

Figure 2. Strict consensus tree of Quiinaceae retrieved from a primary cladistic analysis applying equal weights to morphological characters (Tables 1 and 2), and a subsequent secondary analysis using successive weighting. The analyses yielded 1643 trees (163 steps, CI: 0.561, RI: 0.775) and two most-parsimonious trees, one a subset of the other. Dotted lines indicate collapsed branches in the primary analysis. Jackknife fractions above 50% using equal weights (left) as well as weighted characters (right) from the primary analysis are shown above the branches. Below branches are Bremer support values, i.e., additional steps needed to collapse a node for unweighted characters (left), and weighted and rescaled characters (right).

view that apocarpy is derived (see Endress, 1982; Kubitzki, 1995 pers. comm.), could not be observed. Nevertheless, according to the present analysis, this character state is considered a synapomorphy for *Froesia*.

The cladistic analysis indicates an isolated position for *Froesia* in terms of morphology. Support for the genus is strong with no less than eight synapomorphies (Fig. 3). These results correspond to the findings of Gottwald and Parameswaran (1967), who even proposed, based on anatomical studies, the establishment of a separate subfamily for *Froesia*. Besides the apocarpous gynoecium, deeply divided stipules with setaceous lobes (in all but one

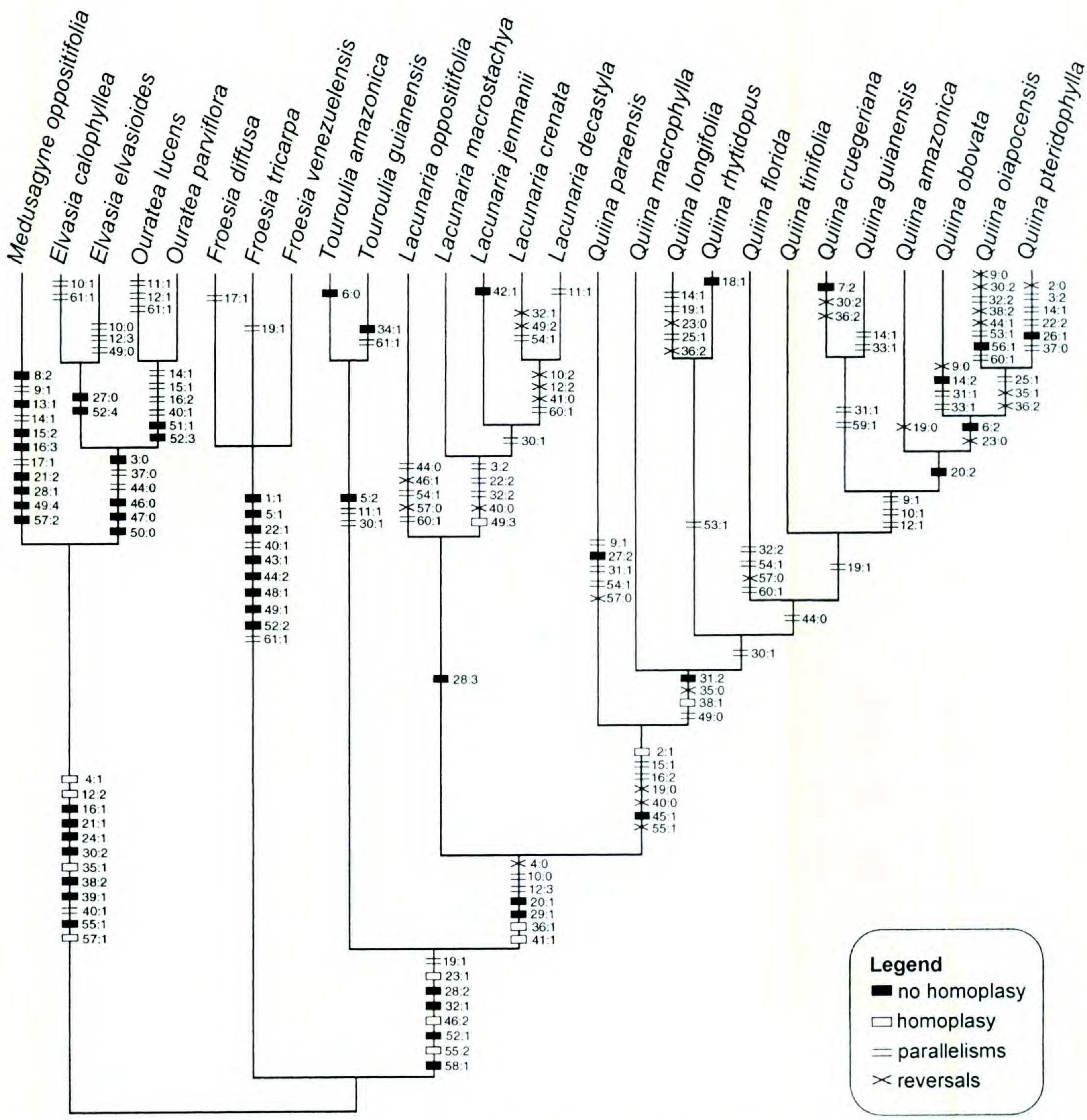

Figure 3. One of the two most-parsimonious trees from the successive weighting analysis of the Quiinaceae with characters optimized on the branches (number left of colon = character; right = character state, cf. Table 1).

species), glabrous seeds, and hermaphroditic flowers are important characters to distinguish the genus. This example addresses the importance of including autapomorphies in phylogenetic analyses, following Yeates (1992). If only one *Froesia* species had been included, a number of characters would have been regarded as autapomorphies, uninformative, excluded, and hence probably overlooked as potential synapomorphic characters for the genus.

Apart from *Froesia*, the remaining species of Quiinaceae are distinguished by several synapomorphies, including the evolution of staminate flowers (char. 28: 2), their position in small terminal groups (char. 32: 1), a berry-like fruit (char. 52: 1), and pubescent seeds (char. 58: 1). *Touroulia* forms a monophyletic group and is recognized by only one synapomorphy, the compound leaves with an alate rachis (char. 5: 2). As previously mentioned, generic rank was proposed for *T. amazonica* (Pires, in sched.), a view also advocated by Gottwald and Parameswaran (1967) based on their anatomical studies. Nevertheless, from a morphological point of view, the two *Touroulia* species are very similar (Zizka & Schneider, 1999), confirmed by the present analysis, and, hence, Pires's proposal is rejected.

A number of characters unite the genera *Quiina*

and *Lacunaria*. Polymorphic characters such as the position of the inflorescence (char. 29) in *Lacunaria* are interpreted as inconclusive of relationship (soft starts sensu Kornet and Turner, 1999). Regarding *Lacunaria*, conflicting data fail to conclusively resolve the taxa in the analysis using equal weights, but support for *Quiina* is strong. However, a phylogenetic signal for *Lacunaria* is picked up if the approach to character weighting is used, gaining a fully resolved tree, but with very low support values. A jackknife value of 61% and a rescaled Bremer support value of 0.9 cannot be considered as much support for a monophyletic genus. Based on the weighted analysis, a possible single synapomorphy is identified for *Lacunaria* (char. 28: 3). Most other characters are homoplastic within the genus, and some are also observed in, for example, *Quiina pteridophylla*. Our knowledge of interrelationships within *Lacunaria* is not satisfactory, but pending future analysis we refrain here from proposing any systematic rearrangement and treat the genus in its traditional circumscription.

Two characters, verticillate leaves (char. 3: 2) and completely fused stipules (char. 22: 2), have evolved in the clades of *Lacunaria* and *Quiina*. Based on our morphological studies, *Quiina pteridophylla* was expected to be closely related to *Lacunaria*. The present analysis indicates that *Q. pteridophylla* shares almost all other generic characters and that it is deeply nested within *Quiina* rather than having a basal position in the genus. Forcing a sister relationship of *Q. pteridophylla* with *L. oppositifolia*, which it superficially resembles, costs no less than 10 extra steps. Thus, there is no doubt that these two species are not closely related and cannot form a sister relationship.

Reasons for previous hypotheses of recognizing *Lacunaria oppositifolia* at generic rank can here be understood. Following the weighted analysis and tracing character evolution (Fig. 3), the species forms a clearly distinct branch with no less than five homoplastic characters. The remaining lineage of *Lacunaria* has, interpreted from the tree in Figure 3, gained the same number of homoplastic characters, although they are different. Although a monophyletic genus can be envisioned, there is also weak jackknife support for *L. oppositifolia* forming a separate lineage nested between *Lacunaria* s. str. and *Quiina* if equal weights are used. One option is to include *L. oppositifolia* in *Quiina*, but this solution is not attractive because a morphologically well circumscribed group would be lost. Leaf venation pattern, the absence of intersecondary veins, and the number of carpels do not coincide with the generic concept of *Quiina*. Moreover, cladistic support of the genus *Quiina* is almost four times as strong as the next internal node. A second solution is to describe a monotypic taxon, but due to the weak support, and not appearing in the consensus, the issue of the rank and position of *L. oppositifolia* has to be postponed until other data, particularly from DNA analyses, are obtained.

Taxa sampled of *Quiina* for this analysis include about one third of the total number of the species. As a genus, *Quiina* is rather well supported, but support clearly increases after successive weighting. A cursory inspection of Figure 3 also reveals a number of reversals and parallelisms on branches leading to the terminals, especially in the most advanced part of the tree. We interpret this, in conjunction with a high ratio of polymorphic characters, to indicate that novelties are allowed to rise and spread within the lineage. They represent soft reversals without hard starts of character states (Kornet & Turner, 1999). Two reasons, and possibly more, explain this observation. First, the lineage might be fairly young and presently going through numerous speciation events without character state fixation. Second, interpretations of our character states may be incorrect, i.e., misinterpretation of homologies.

EVOLUTION OF ANDRODIOECY

Different modes of sex distribution in the Quiinaceae—androdioecy in *Quiina* and *Touroulia*, dioecy in *Lacunaria*—seem to have evolved from a hermaphroditic ancestor. Hermaphroditism is the plesiomorphic state, found in the basal genus *Froesia* and in the outgroup Ochnaceae. Andromonoecy is an autapomorphy for the outgroup taxon *Medusagyne* and is not further considered herein. Androdioecy (char. 28: 2) is a synapomorphy within Quiinaceae that evolved, in a phylogenetic perspective, in the following pathway: androdioecy is the plesiomorphic state and dioecy independently evolved in *Lacunaria*.

Concerning the evolution of androdioecy and dioecy, several models have been formulated (Ross, 1978, 1982; Thomson & Barrett, 1981; Charlesworth, 1984; Thomson & Brunet, 1990; Richards, 1997; Swensen et al., 1998). The majority regards dioecy as derived from hermaphroditism via androdioecy or gynodioecy (Darwin, 1877; Westergaard, 1958; Bawa, 1980; Richards, 1997). Another model of androdioecy evolution proposed by Ross (1982) is from hermaphroditic flowers via andromonoecy, as observed in some *Solanum* species. However, andromonoecy is only known from the outgroup, *Medusagyne*. In contrast, Swensen et al. (1998) ar-

gued that [functional] androdioecy evolved from dioecy in Datiscaceae. This path is improbable for Quiinaceae since androdioecy evolved once in the ancestor of *Touroulia*, *Lacunaria*, and *Quiina*, with a further reduction to dioecious flowers in *Lacunaria*.

Mechanisms that favor the evolution of androdioecy and dioecy are explained by models of sexual selection and sex allocation, and are discussed by several authors (Ross, 1978, 1982; Bawa, 1980; Thomson & Barrett, 1981; Charlesworth, 1984; Thomson & Brunet, 1990; Richards, 1997; Pannell, 1997). One hypothesis argues that in female-sterile plants the loss of seed production is more than compensated for by the reallocation of resources to increased pollen production (Thomson & Brunet, 1990). This may be achieved through an increased number of staminate flowers or stamens, or through larger anthers. Flower numbers are more or less equal among the Quiinaceae or even lower in the (andro-)dioecious taxa. Anthers are roughly of the same size in the family, hence not serving as a useful argument. The number of stamens, indeed, is generally increased in staminate flowers of *Quiina* and *Touroulia*. Nevertheless, comparing the genera, the stamen numbers do not provide an explanation for the evolution of the observed pattern of sex distribution since the supposedly ancestral hermaphroditic flowers of *Froesia* bear the highest number of stamens within the family. If we trace an evolutionary pathway from hermaphroditism through androdioecy to dioecy, as postulated above, we see a reduction of stamen numbers from more than 100 in *Froesia*, 30 to 80 in *Touroulia*, most *Lacunaria*, and some of the *Quiina* species, to approximately 10 to 25 in *Quiina* and in a few *Lacunaria* species, including *L. oppositifolia*. Thus, other mechanisms such as the avoidance of inbreeding may provide a better explanation for the evolution of dioecy in the present case.

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